How well can body size represent effects of the environment on demographic rates? Disentangling correlated explanatory variables

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Abstract: 1. Demographic rates are shaped by the interaction of past and current environments that individuals in a population experience. Past environments shape individual states via selection and plasticity, and fitness-related traits (e.g. individual size) are commonly used in demographic analyses to represent the effect of past environments on demographic rates. 2. We quantified how well the size of individuals captures the effects of a population's past and current environments on demographic rates in a well-studied experimental system of soil mites. We decomposed these interrelated sources of variation with a novel method of multiple regression that is useful for understanding nonlinear relationships between responses and multicollinear explanatory variables. We graphically present the results using area-proportional Venn diagrams. Our novel method was developed by combining existing methods and expanding upon them. 3. We showed that the strength of size as a proxy for the past environment varied widely among vital rates. For instance, in this organism with an income breeding life history, the environment had more effect on reproduction than individual size, but with substantial overlap indicating that size encompassed some of the effects of the past environment on fecundity. 4. This demonstrates that the strength of size as a proxy for the past environment can vary widely among life-history processes within a species, and this variation should be taken into consideration in trait-based demographic or individual-based approaches that focus on phenotypic traits as state variables. Furthermore, the strength of a proxy will depend on what state variable(s) and what demographic rate is being examined; that is, different measures of body size (e.g. length, volume, mass, fat stores) will be better or worse proxies for various life-history processes.

DOI: https://doi.org/10.1111/1365-2656.12465

How well can body size represent effects of the environment on demographic rates? Disentangling correlated explanatory variables

A manuscript in consideration as a standard paper for publication in Journal of Animal Ecology as part of the Special Feature *Demography beyond the Population*

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Summary

1. Demographic rates are shaped by the interaction of past and current environments that individuals in a population experience. Past environments shape individual states via selection and plasticity, and fitness-related traits (e.g., individual size)

22 are commonly used in demographic analyses to represent the effect of past
23 environments on demographic rates.
24 2. We quantified how well the size of individuals captures the effects of a
25 population's past and current environments on demographic rates in a well-
26 studied experimental system of soil mites. We decomposed these interrelated
27 sources of variation with a novel method of multiple regression that is useful for
28 understanding nonlinear relationships between responses and multicollinear
29 explanatory variables. We graphically present the results using area-
30 proportional Venn diagrams. Our novel method was developed by combining
31 existing methods and expanding upon them.
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33 widely among vital rates. For instance, in this organism with an income
34 breeding life-history, the environment had more effect on reproduction than
35 individual size, but with substantial overlap indicating that size encompassed
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38 vary widely among life-history processes within a species, and this variation
39 should be taken into consideration in trait-based demographic or individual-
40 based approaches that focus on phenotypic traits as state variables. Furthermore,
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43 length, volume, mass, fat stores) will be better or worse proxies for various life-
44 history processes.
45

Key-words adaptation, demographic rates, environmental effects, multicollinearity, multiple regression, trait-based demography, area-proportional Venn diagram

Introduction

The past and current environments experienced by individuals shape their demographic rates, and these effects can be partially captured in individual state variables such as body condition, mass, and size (Easterling, Ellner & Dixon 2000; Caswell 2001; Benton, Plaistow & Coulson 2006). For many species, size-at-age, body-mass-index, or fat reserves are influenced by food availability and relate to patterns of resource acquisition and storage (Kooijman 2000). Size can be a good proxy for an individual's general state including developmental stage, resource acquisition and stores, and the outcomes of competitive interactions (Peters 1986). Past experiences shape an individual's current state, and current state interacts with the current environment to determine the individual fate (i.e., survival, growth, and reproduction). An individual's full multifaceted state includes its genotype, phenotype, epigenetics, energy reserves and many other variables that can be difficult to measure. Recent research on trait-based demography has highlighted the power of including easy to measure state variables such as individual size in demographic models including matrix and integral projection models (IPMs) (Easterling *et al.* 2000; Caswell 2001; Ozgul *et al.* 2009; 2010) and agent-based models (Grimm *et al.* 2006). However, how much of the past and current environmental effects on demographic rates are captured by individual size and how much variation is left to be explained has not been explored as thoroughly and directly as we aim to here.

The dynamics of state variables and demographic rates are shaped by selection, phenotypic plasticity, and parental effects (Ozgul *et al.* 2010; Coulson *et al.*

2011; Benton 2011; Ozgul *et al.* 2012). In many cases, much of the cumulative effects of the past and current environments on demographic rates are integrated into an individual's size (or condition), but not all (Festa-Bianchet, Gaillard & Jorgenson 1998; Ozgul *et al.* 2010; DeLong, Hanley & Vasseur 2014). For example, in bighorn sheep, which are considered to be capital breeders, body mass reflects the amount of stored resources available for reproductive effort. Yet, a positive effect of body mass on female reproductive success was only evident at high population densities, a biotic component of the current environment resulting from conditions in the past environment (Festa-Bianchet et al. 1998).

Such cases of weak or context-dependent relationships between an individual's state and demographic rates can arise from differences in the sensitivity of life-history traits to past and current environments (Le Galliard et al. 2010; Beckerman et al. 2003; Taborsky 2006). Such differences can be due to the fact that selection, plasticity, and parental effects do not affect traits equally (Benton *et al.* 2006). In addition, context-dependent associations between traits can arise from changes in life-history trade-offs in response to environmental variation that affect patterns of covariation between life-history traits throughout time (e.g., Plaistow et al. 2006; Plaistow and Benton 2009). These examples highlight the complex array of potentially interacting mechanisms shaping life-history and population dynamics and the importance of investigating how much of this variation can be summarized into one easily observable, individual condition-index such as body size (Beckerman *et al.* 2002; Benton *et al.* 2006; Evans *et al.* 2013).

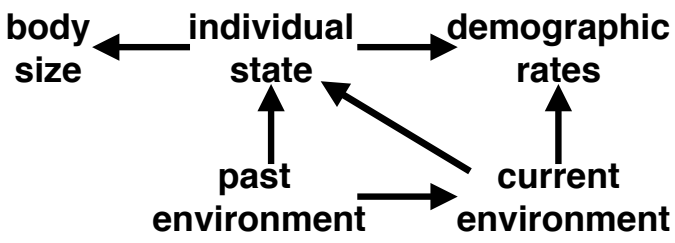


Fig. 1. Influence diagram. Arrows indicate the influence of demographic components on each other. Past environments influence the current environment by shaping the demographic structure and population density. Past environments influence individual states via natural selection, plasticity, and maternal effects. We observe part of an individual's multifaceted state via its body size. In the soil mite model system, past environments include those an individual has experienced, but also those experienced by maternal, grand maternal and great-grand-maternal generations (Plaistow, Lapsley & Benton 2006).

In this study, we used an extensive laboratory experiment to characterize how demographic rates changed through time in populations experiencing drastically different environments. Our model organism, *Sancassania berlesei* (a soil mite), has a life-history that plastically responds to food availability and population density, and exhibits maternal effects (Benton, Lapsley & Beckerman 2001; Benton, St Clair & Plaistow 2008; Ozgul *et al.* 2012). This experiment enabled us to quantify the influence of individual body size, current environment, and past environment on demographic rates.

Favorable past and current environments lead to better individual states and thus enhanced demographic rates, but a favorable past environment increases population density and can thus reduce the quality of the current environment. The interdependencies of body size, current environment, and past environment (Fig. 1) cause multicollinearity (i.e., correlation) among explanatory variables in regression models that makes it difficult to disentangle the effects (Graham 2003). To disentangle the influence of body size, the current environment, and the past environment, we have used a novel procedure based on the practice of fitting all

119 possible subsets of these multicollinear explanatory variables (Chevan & Sutherland
120 1991; Graham 2003; Murtaugh 2009). We modeled potentially nonlinear effects of
121 these explanatory variables on demographic rates using splines (Dahlgren, Garcia &
122 Ehrlén 2011). We teased apart the overlap in explanatory power by comparing the
123 proportion of deviance explained (a generalization of r^2, Wood 2006) from models
124 with all subsets of explanatory variables. Overlap in explanatory power is a result of
125 multicollinearity among the explanatory variables, caused by the interdependencies
126 described above. This method is novel because it disentangles multicollinearity in
127 nonlinear splines in a way previously used for linear models (Ip 2001). Also, this
128 paper is the first to plot the results of this decomposition using area-proportional Venn
129 diagrams which are visually intuitive (Micallef & Rodgers 2014). Our goal was to
130 quantify how well the past and current environmental effects on demographic rates
131 were represented by body size, and how much variation was left to be explained.
132 In the past, researchers have attempted traditional time series decomposition of
133 measured phenotypes in *Sancassania berlesei* and how they change over time (Benton
134 *et al.* 2005) but this is complex because the importance of the past environments vary
135 over time in a way that is itself context dependent (Beckerman *et al.* 2003; Plaistow *et*
136 *al.* 2006; 2007). So standard linear time series models are not informative. Our new
137 method of decomposing the variability in demographic rates is therefore valuable as it
138 can highlight the importance of processes that we know to be sensitive to conditions
139 in complex ways. Most importantly, it challenges one major assumption underlying
140 recently popular trait-based demographic models: that a focal state variable such as
141 body size captures the effects of past and current environments on the individual's
142 performance, and acts as a memory mechanism to project the individual performance
143 to future time steps. By using a well-studied system we can benchmark the

144 performance of the new technique. If the technique produces results that match our
145 detailed understanding of this model system, we can have confidence that it has utility
146 for studying systems where the background knowledge is lower.

147 In the following text, we first describe our methods including the experiment
148 for our soil mite case study and then statistical analyses including hypothesis testing
149 and variance decomposition. Then we present results from the case study and divide
150 our discussion into a soil mite specific discussion and a discussion of the general
151 applicability of our method for both demographic and general ecological studies.

152 ## Materials and methods

153 ### *Experimental Methods*

154 The goal of our experiment was to observe how population dynamics and
155 individual demographic rates change in response to vastly different environments that
156 should induce selection, plasticity, and maternal effects.

157 Populations of soil mites were raised in 22 mm diameter tubes for nine weeks
158 in four environments: one constant (control) and three varying (famine, declining, and
159 fluctuating). Famine and fluctuating populations experienced abrupt changes in their
160 food (Fig. 2). The experimental timespan is approximately two times the generation
161 time of soil mites maintained in food conditions similar to our control treatment
162 (Ozgul *et al.* 2012; Cameron *et al.* 2013). Treatments differed in the amount of food
163 provided and subsequently, population densities naturally varied accordingly (Fig. 2).
164 All populations experienced a constant food environment prior to the experiment until
165 population dynamics and stage structure stabilized. The life stages are as follows (in
166 order): egg, larva, protonymph, tritonymph, and adult (male or female).

167 There were two replicate sampling populations and five replicate counting
168 populations per treatment. The counting populations were censused twice per week to

monitor population density and stage structure. There were twenty-eight populations total; more replicates were not possible due to the work required for censusing the counting populations. Twice per week per sampling population, five adult males and five adult females were sampled and placed in five mixed-sex tubes for a period of 24 hours; also three individuals from each juvenile stage (larva, protonymph, tritonymph) were placed in three mixed-stage tubes for a period of 24 hours. Sampling was done several hours after feeding. Sampled individuals were photographed before and after the 24-hour period in which the following responses were monitored: survival (binary), final body length (mm), stage transition (binary), reproduction (binary and egg counts). After the 24-hour monitoring period, surviving individuals were put back in the sampling populations. Eggs were not put back because of the time required to move eggs 0.18 mm in diameter. See appendix S1 for more experimental details.

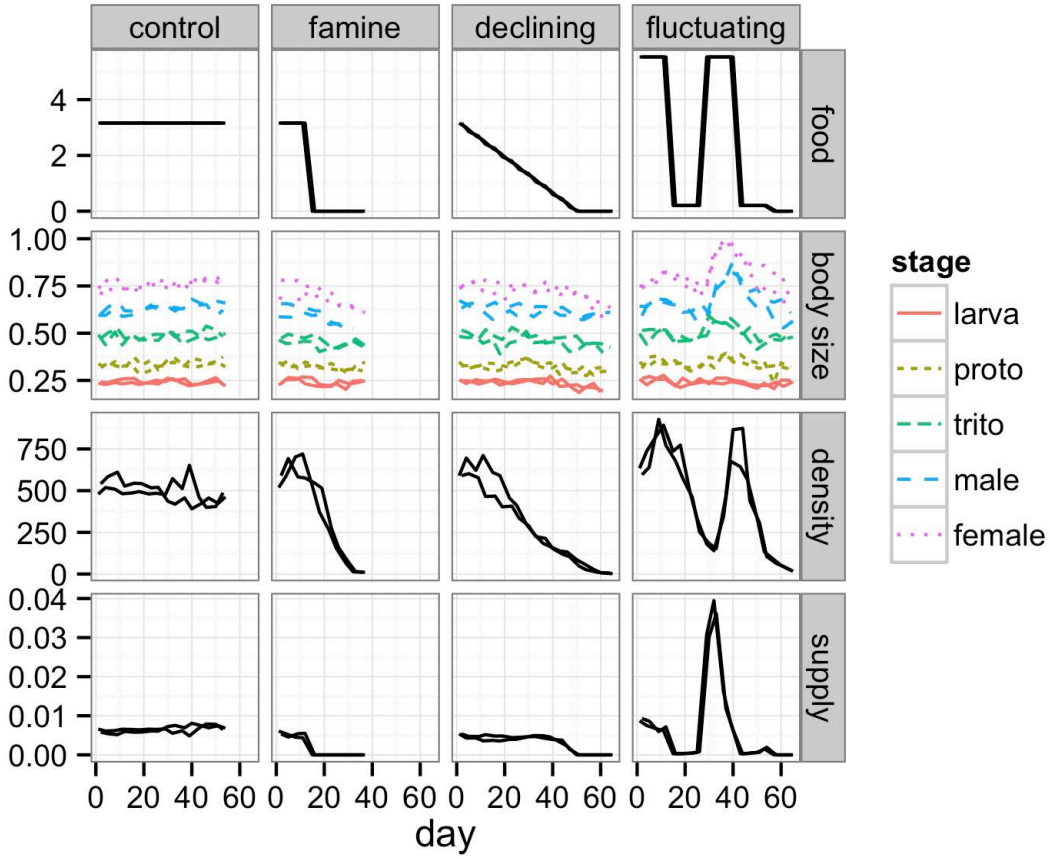


Fig. 2. Experimental environments and demographic covariates. Each column is a different experimental treatment with two populations per treatment each represented by a line. Each row represents a different covariate: food provided (in mg), naturally varying average individual body size at start of monitoring (length in mm), population density weighted by the average body size in each stage (i.e., total body length per tube), and food supply (food divided by density, i.e., mg food per mm body length). The number of individuals per density unit is equal to the inverse of the stage-specific average length: approximately 4.3 larvae, 3.1 protonymphs, 2.2 tritonymphs, 1.6 males, or 1.4 females, but this varies throughout the experiment as body sizes vary.

Statistical Methods

The goals of our statistical analyses were to determine which demographic responses (i.e., life-history processes) depended on starting body size, current environment, and past environment; then to determine the power of these explanatory variables and how much power overlapped due to multicollinearity.

We quantified evidence of the influence of starting body size, current environment, and past environment on demographic responses using generalized additive mixed models (GAMMs). We used GAMMs because demographic responses potentially have nonlinear dependence on starting body size (Anderson *et al.* 2008; Dahlgren *et al.* 2011; Ozgul *et al.* 2012; Cameron *et al.* 2013) and we expected responses to change nonlinearly during the experiment in response to the environment. Generalized additive models (GAMs) are convenient because they do not require that one makes assumptions about the shape of the nonlinear relationships. They are generalized linear models that represent the nonlinear relationship using smooth functions of covariates (Wood 2006). GAMMs are GAMs with random

207 effects in addition to fixed effects, which we use here to account for repeated
208 measures of populations.

209 Demographic responses of interest were measured after 24 hours for mites
210 sampled from the population (see Experimental Methods). Responses included final
211 body size (length in mm), initiation of transition from one developmental stage to the
212 next (binary), reproduction by females (binary), fecundity (number of eggs laid given
213 reproduction), egg size (in mm, average within female), and survival. In trait-based
214 demography, it is common to model the growth process as an individual's size at the
215 end of a time step dependent on its size at the start of the time step, so we follow that
216 standard and use "final body size" and "growth" interchangeably.

217 Explanatory variables of interest included starting life-history stage (the stage
218 of an individual at the start of a 24-hour monitoring period), starting body size,
219 current environment, and past environment; see the following three paragraphs for
220 further descriptions of starting body size, current environment, and past environment
221 (Fig. 1). For clarity, we consistently refer to these four components as "explanatory
222 variables". Alternatively, we use "covariates" to refer to the observed variables
223 included in the smooth functions that make up these explanatory variables.

224 The explanatory variable "body size" (i.e., starting body size) was a smooth
225 function of an individual's observed body size at the start of the 24-hour monitoring
226 period. Throughout this text, all discussions of the explanatory power of body size are
227 referring to this starting body size explanatory variable.

228 The explanatory variable "current environment" was a two-dimensional
229 smooth function of the most recent estimate of (i.e., within the past 24 hours)
230 population density and food supply (used here to mean food given divided by density;
231 density and food supply are further described below). Two-dimensional smooth

functions allow for nonlinear effects of the covariates and their interaction. The fit of a two-dimensional smooth function results in a three-dimensional nonlinear surface, the height (i.e., third dimension) of which represents how the response variable changes with the covariates. We assumed that the current environment experienced by an individual is an interaction between the population density and the available food. Population density (per tube) was calculated as the number of individuals in a given stage times the average body size in that stage, summed across all stages, except eggs, to account for asymmetric competition. See appendix S2 for details of our density calculations. Food supply (food given divided by density, i.e., mg food per mm body length) was used as a covariate (as part of the current environment smooth function) instead of absolute food because preliminary analyses indicated that it was a better predictor of all demographic responses.

The explanatory variable "past environment" was a treatment intercept and a smooth function of the day of each treatment. When specifying a smooth function of a continuous variable by a categorical variable in a GAM (as in our past environment by treatment), it is usually necessary to include a separate intercept for that categorical variable. Our treatment intercepts are parameterized in the standard way with the control treatment as a baseline and other treatments as contrasts. The smooth functions of time are not tied to any informative covariates and can take any nonlinear shapes that are smooth through time and thus account for cumulative changes in demographic responses that arise through selection, plasticity, or parental effects. This flexibility can incorporate the cumulative effects of the environment up to the moment a demographic response is observed which encompasses much of what we call the "current environment" i.e., the most recently estimated population density and food supply. Thus, effects of the environment before this "current environment" should be

257 evident in explanatory power from the “past environment” that does not overlap that
258 of the “current environment”. The “past environment” spline was defined in such a
259 flexible way so that, in a full model with all explanatory variables, it can pick up any
260 population level patterns not explained by individual body size, population density, or
261 food supply. This implies that, given two individuals of the same body size in the
262 same current environment in different treatments or different times in the same
263 treatment, we assume that any differences in their demographic rates are caused by
264 differences in their past environments. It is possible that there are aspects of the
265 current environment that differ, but are not incorporated into our current environment
266 spline. So this interpretation of the residual patterns is not strong evidence but a
267 means of generating hypotheses that could be tested with further experiments that are
268 more mechanistic.

269 For example, the full GAMM fit to egg counts (fecundity) contained a smooth
270 function of starting body size, a treatment intercept, a smooth function of the day for
271 each treatment, a two-dimensional smooth function of the population density and food
272 supply, and a random effect of population. The hypothesis represented by this model
273 is that an individual’s fecundity depends on its current access to food and the body
274 size of that focal individual (which determines its competitive ability). However, the
275 allocation strategy of individuals in some treatments or time points of treatments may
276 differ from individuals of similar size in similar current environments due to differing
277 past environmental experiences. These differences due to past environmental
278 experiences should appear in the non-overlapping explanatory power of the past
279 environment spline.

280 To be clear, as part of the GAM fitting procedure, the smooth functions
281 described above took on different nonlinear shapes (thin-plate regression splines) for

each model just as coefficients would differ among linear models. Variation in a demographic response can be explained by one explanatory variable in one model and a different explanatory variable in a different model that contains a different set of variables. This is the same issue that occurs when estimating coefficients in linear multiple regression with correlated explanatory variables (Chevan & Sutherland 1991; Graham 2003). Multicollinearity hinders the interpretability of the coefficients and smooth functions (Mitchell-Olds & Shaw 1987).

For each demographic response separately, we fit the full GAMM containing all explanatory variables described above. We applied Wald-type tests to the full GAMM (Wood 2013b); these are p-values indicating the strength of evidence against the null hypothesis that explanatory variables have no influence. We also examined all submodels of the full GAMM using information theory and results were similar to the Wald-type tests; the details including R code can be found in appendix S3.

For demographic responses whose supported explanatory variables contained starting body size, current environment, or past environment we calculated the explanatory power of each of these and their overlap. We focused on these explanatory variables because they were relevant to all responses whereas life-history stage only applies to some responses and may not apply to all species. Unlike models that tested for effects, to simplify the interpretation of explanatory power, these contained no random effect. It is possible to expand this method to apply to mixed models, but this is beyond the scope of this paper (Nakagawa & Schielzeth 2012). We fit GAMs with all subsets of the supported explanatory variables. We calculated the overlap in explanatory power as the difference from what the explanatory power of a model with multiple variables would be if it were additive relative to single variable models. The non-overlapping explanatory power is the increase in

307 explanatory power when adding a variable to a model that already contains other
308 variables. These calculations have been previously described for variance partitioning
309 in linear models (Chevan & Sutherland 1991; Ip 2001; Grömping 2007).

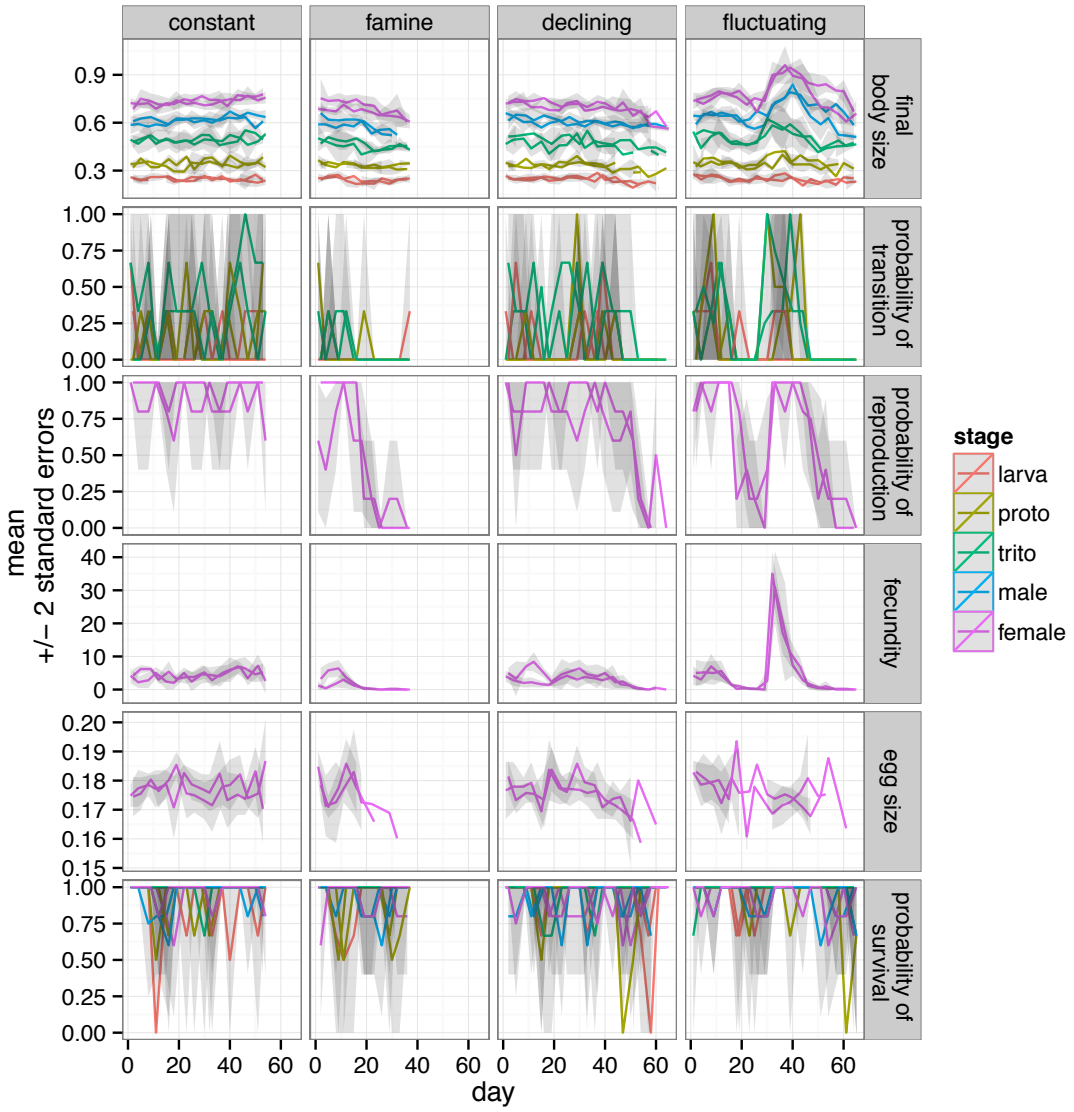
310 Other statistical methods exist for dealing with multicollinearity, but they do
311 not address our interest in interpreting both the overlapping and non-overlapping
312 portions of explanatory power to get insight into the demographic processes that lead
313 to multicollinearity (Graham 2003). Principal components analysis takes many
314 predictors and summarizes them into just a few, but we wanted to look at all of the
315 predictors and their relationship with body size. Residual and sequential regression
316 require that you assume some hierarchy among the explanatory variables, but we
317 wanted to see if body size was more important, not assume it. Structural equation
318 modeling and path analysis can not handle relationships as flexibly as GAMs and we
319 wanted our method to be able to pick up minor nonlinearities in the time series
320 (Brandt, Kelava & Klein 2014). For these reasons, we have expanded upon existing
321 methods and combined existing tools in new ways to produce a new method for
322 examining multicollinear predictors that have nonlinear relationships with the
323 response variable.

324 All GAMMs were fit in R using gamm4 with lme4 and GAMs were fit using
325 mgcv (Wood 2013a; Bates *et al.* 2013; Wood & Scheipl 2013). For smooth functions,
326 we used penalized thin-plate regression splines that tend to give the best mean squared
327 error (Wood 2003; 2013a). All continuous covariates except day were standardized to
328 have mean zero and unit variance. We allowed smooth functions of starting body size,
329 current environment, and past environment to have a maximum of five, ten, and ten
330 knots respectively. Five knots for the effect of starting body size were previously
331 discussed by (Dahlgren et al. 2011). Because current environment was a two-

dimensional spline, we assumed it might need more knots. Examination of the responses (Fig. 3) suggested that they might be more flexible through time (i.e., past environment). The mgcv package automatically reduces the flexibility of splines based on maximum likelihood using the Laplace approximation. All models used typical distributions and link functions for the responses as follows: final body size was Gaussian (identity link); stage transition was binomial (logit link); reproduction was binomial (logit link); non-zero fecundity minus one was Poisson (log link); survival was binomial (logit link).

Results

In each experimental environment, demographic responses varied through time and with some consistency between the two replicate populations (Fig. 3). Wald-type tests applied to the full model indicated that starting body size and the current environment had effects on most demographic rates (Table 1). Development and reproductive rates were higher for individuals with larger body sizes and in environments with higher food supply (appendix S5). Higher density decreased growth and reproductive rates, but had a positive effect on transition probability with marginal significance (Table 1 and appendix S5). While controlling for the effects of body size and the current environment, declining and fluctuating environments also caused temporal patterns for some demographic rates (Table 1 and appendix S5).



352

353 **Fig. 3. Observed life-history processes.**

354 Each column represents an experimental treatment. Each row represents a life-history
355 process observed over a 24 hour monitoring period: final body size at the end of
356 monitoring (length in mm), probability of initiating transition from one developmental
357 stage to the next, probability of reproduction (given female), fecundity (number of
358 eggs laid given reproduction), egg size (in mm, average within female), and survival.
359 Lines represent the mean of individuals sampled from a population on a given day (a
360 subset of the population: 5 from each adult stage and 3 from each juvenile stage).
361 Grey ribbons represent +/- 2 standard errors. Standard errors are missing for egg size

362 on days when only one female was sampled. Observations in the famine populations
363 ended when all individuals died. The control populations persisted to the end, but
364 observations ended. ‘Proto’ refers to protonymph and ‘trito’ to tritonymph.
365

366 **Table 1:** Wald-type tests (to test the null hypothesis that the smooth function was not
367 different from 0) applied to all smooth functions in the full GAMMs. The control
368 intercept was used as the baseline for treatment contrasts and was always non-zero
369 (***). The growth model containing stage gave a convergence warning, so we omitted
370 it (see appendix S3 for details). 'NA' indicates that stage was not included in a model
371 to distinguish this case from non-significance. 'Proto' refers to protonymph and 'trito'
372 to tritonymph.
373 '.' p<0.1, '*' p<0.05, '**' p<0.01, '***' p<0.001

	Stage	Body size	Current environment	Past environment smooth functions (and intercept in parentheses)			
				Control	Famine	Declining	Fluctuating
Growth	NA	***	***				* (.)
Transition	***(proto) ***(trito)	***	.			.	** (***)
Reproduction	NA	***	***		(*)	**	(***)
Fecundity	NA	***	***			**(**)	(.)
Egg Size	NA				(.)	*	*
Survival	*(trito)						

374
375

Power of supported explanatory variables

The best explanatory variable of growth and stage transition was body size (Fig. 4). Both reproductive rates depended more on the environment than on female body size (Fig. 3). Body size encompassed almost all of the explanatory power of the current and past environments for growth (0.99); 0.27 and 0.26 respectively for stage transition; 0.39 and 0.34 respectively for reproduction; and 0.47 and .48 for fecundity (numbers are proportion of explanatory power overlapping). See Appendix S4 for explanatory power calculations. As is common for variance decompositions, some shares came out slightly negative so we rounded these to zero for graphing in Fig. 4 (Hamilton 1987; Ip 2001); these were an order of magnitude smaller than the portions we interpret (Growth: se=-0.001; Transition: se=-0.007, sh=-0.005). This indicates that one variable was masking a tiny amount of the explanatory power of another variable (Hamilton 1987). This omission is why the subareas do not perfectly add up.

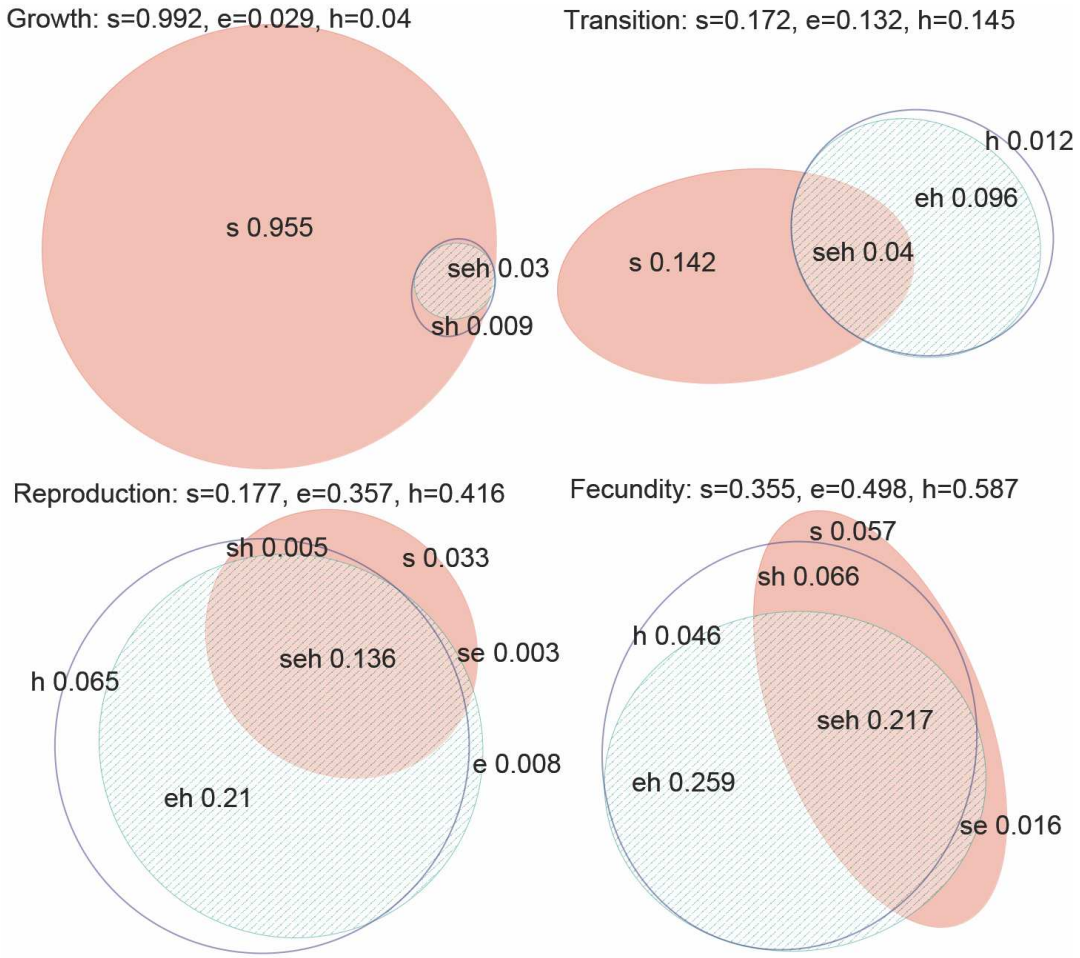


Fig. 4. Overlapping explanatory power of starting body size (s), current environment (e), and past environment (h). Each panel contains an area-proportional Venn diagram (Micallef & Rodgers 2014) of explanatory power for a demographic response: final body size after 24 hours (Growth), probability of initiating stage transition (Transition), probability of reproducing (Reproduction), and Fecundity. Areas of the ellipses within a panel represent the proportion of null deviance explained by models with one of the explanatory variables. Subareas, designated with letters and quantities, represent explanatory power attributable to one, two, or three of the explanatory variables due to interdependence of the variables. Labels of zero areas were omitted. The total explanatory power of a component is the sum of the subareas, noted at the top of each panel. See Appendix S4 for calculations.

Discussion

Predicting life-history and population responses to changing environments has long been the focus of population ecologists (e.g., Williams 1966). Trait-based demographic models have highlighted the strength of including state variables such as body size to understand and predict population dynamics (Easterling et al. 2000; Caswell 2001; Ozgul et al. 2010). However, these models rely on the assumption that chosen state variables are a good proxy of the effects of the environment on demographic rates. Here, we challenged this assumption by investigating how well body size represented the integrated effects of environmental sequences by quantifying the dependence of demographic responses on individual body size, current environment, and past environment in a well-studied soil mite experimental system. To do so, we used a quantitative method for decomposing the effects of multicollinear explanatory variables, extended to allow for nonlinear relationships and graphically presented using area-proportional Venn diagrams.

The past environment explanatory variable was designed to pick up population level patterns after controlling for the effects of body size and the current environment. This should include delayed effects from past environments experienced by individuals and their mothers. Although not all of these splines were significantly different from zero, examining the patterns is useful for generating hypotheses to be investigated with more detailed data and more mechanistic models. Here, we demonstrate this with the soil mite model system because many mechanisms are already known.

We found that the total explanatory power of body size and the amount of environmental effects encompassed by body size strongly varies among demographic responses. Although this general result is already known, we demonstrate that the

strength of our method lies in its flexibility, making it easily applicable to data limited situations, which are common in ecology. It is a useful tool to identify patterns and test for the ability of state variables to encompass environmental effects on demographic and life-history responses that can later be explored with more mechanistic experiments.

The case of soil mite populations in drastically different environments

Developmental rates depended more on body size than past or current environments, and reproductive rates were more strongly affected by the environments than by body size. For final body size (i.e., growth), the effect of the environment was almost fully encompassed by starting body size, while for other demographic responses, body size only accounted for a quarter to half of the environmental explanatory power. These results demonstrate that demographic responses differed in their sensitivity to the environment and the proportion of environmental effects transmitted through an individual's body size (e.g., Ozgul et al. 2012; Ozgul et al. 2010).

We expected to find significant effects of the past environment on developmental rates because previous work demonstrated that soil mites can exhibit strong delayed life-history effects in response to densities and food regimes (Beckerman et al. 2003; Plaistow et al. 2006; Cameron et al. 2013). However, in our experiment, these effects were almost completely overlapped by the current environment. Previous experiments, that found effects of past environments on development rates utilized very different food levels (high *vs* low food for individuals, or stochastically varying food with high frequency for populations) (Beckerman et al. 2003; Plaistow et al. 2006; Cameron et al. 2013). In the current experiment, on a daily

453 basis, food and population density was strongly autocorrelated, meaning that current
454 and previous environments were on average similar across the experiments. Under
455 these conditions, the impact of current conditions on developmental rates was very
456 strong. One exception was in the fluctuating environment where, after controlling for
457 the effects of body size and the current environment, developmental rates declined
458 over time (supplementary Fig. S1). This could be due to delayed density dependence
459 driven by the high densities during the first 3 weeks of the experiments in response to
460 the first peak of food availability (Beckerman et al 2003, Benton et al 2005). Cohorts
461 of juveniles born under high densities grow and develop slowly and can only recruit
462 when competition for food is very low (Benton et al 2005). In the fluctuating
463 treatment, competition for food was very low at the beginning of the second peak of
464 food availability, when density was low, leading to a peak of fecundity and generating
465 a new cohort of juveniles born under even higher densities.

466 As expected, our results indicate that females adjusted their reproductive effort
467 according to their environment more than their current body condition (Fig. 4).
468 Reproduction increased with food availability, which was especially evident in the
469 fluctuating environment where a ten-fold rise in reproduction coincided with a spike
470 in food supply (Figs 2 and 3). For both reproductive rates, the explanatory power of
471 the environment not encompassed by body size was substantial (Fig. 4). Under these
472 experimental conditions, female soil mites were on the income breeding end of the
473 income to capital breeding life-history continuum, relying more on current income
474 than on stored resources for reproduction (Stearns 1989). However, we know that
475 under conditions where food differs radically between different parts of the life-
476 history, females raised in low food environments are lower quality and when given
477 excess food as adults are much less fecund than females raised in high food

478 environments (Beckerman, Benton et al. 2003). It is possible that the duration of our
479 fluctuating food experiment was not long enough to observe the effects of this.

480 We hypothesized in Fig. 1 that the past environment can affect demography
481 via the individual's state. We can observe this as an overlap between the explanatory
482 power of body size and the past environment. Interestingly, fecundity showed
483 substantial overlap between these two components. So a portion of the effects of the
484 past environment experienced by a female and her ancestors (effects we know exist in
485 this model organism) were integrated into body size.

486 After accounting for the effects of body size and current environment, the
487 gradually declining environment further reduced both reproductive rates. Also, the
488 past environment had 6% non-overlapping explanatory power. Together, these results
489 support previous findings that females adjust their reproduction through a
490 combination of evolutionary, plastic, and maternal effects in addition to their current
491 environment and condition (e.g., Plaistow et al. 2007; Benton and Plaistow 2008,
492 Cameron et al 2013).

493 ***Unexplained demographic rates in the soil mite case study***

494 Observed daily survival of individuals was independent of environments and
495 body size and may have been artificially high due to reduced density dependent
496 effects during the 24h of sampling. Maternal effects on egg size were not observed in
497 this experiment, but effects may have been transmitted through unobserved pathways
498 such as epigenetics (Youngson & Whitelaw 2008) or nutrient investment (Benton et
499 al. 2008). Transition rates only responded to the environment with marginal
500 significance. Although our experimental design did not allow for collection of further
501 data, the estimation of some of the vital rates can be improved by increasing the
502 sample sizes in future experiments (Fig. 3).

503

504 ***General applicability***

505 The soil mite *S. berlesei* is an attractive model system because much is known
506 about the potential interplay between current and past environments in determining
507 phenotypic variation (Beckerman *et al.* 2003; Plaistow *et al.* 2006; 2007); yet a
508 critical conclusion from the detailed work on individuals under controlled conditions
509 is that the interaction between current and past environments to determine the
510 phenotype is itself highly plastic. The purpose of this investigation was not to develop
511 a mechanistic understanding of an already well-studied system. Instead, this new
512 variance decomposition method is useful because it is a way of generating an overall
513 picture across a range of environments, of the average interplay between historical
514 and current drivers of phenotypic dynamics.

515 More generally, this method is useful for examining the shared and unique
516 contributions in multiple regression beyond demographic studies, including linear and
517 generalized linear regression. Researchers often wonder which explanatory variables
518 have the greatest influence on their responses – a complicated issue when there is
519 multicollinearity among explanatory variables (Graham 2003). The method described
520 by Ip (2001) and used here for intuitively visualizing the shared explanatory power
521 and interdependence of variables has not yet been adopted by the ecological literature.
522 Here we have expanded upon this method by applying it to nonlinear regression using
523 GAMs rather than linear regression and presenting the results using area-proportional
524 Venn diagrams (Micallef & Rodgers 2014). We propose this method as a technique
525 complementary to those discussed by Graham (2003), including principal components
526 regression, structural equation modeling, and residual and sequential regression.

527 Future work could extend this method further to include confidence intervals
528 estimated by bootstrapping.

529 In demographic studies, there are more mechanistic ways of quantifying the
530 effects of the environment and individual states on life-history processes and
531 population dynamics than our method. More mechanistic methods will lead to
532 stronger inference and the ability to make predictions. These include physiologically
533 structured population models which characterize individuals based on multiple
534 physiological traits such as their size, age, stage, and energy reserves (de Roos 1997).
535 They also include mechanisms such as the consumption and digestion of resources.
536 These models require either data detailed enough to parameterize or *a priori*
537 assumptions about the underlying physiological mechanisms. As is the case in most
538 experimental and wildlife population studies, we did not have such detailed data
539 available in this study. However, our non-mechanistic model has the strength of being
540 flexible enough to apply in these data-limited situations and will be useful for
541 identifying patterns and generating hypotheses that can later be explored with more
542 mechanistic models and experiments with more detailed data collection.

543 The demographic method presented here can be applied to any dataset in
544 which an individual state variable, individual fates, and relevant environmental
545 covariates are available for a population in a variable environment, including data
546 from wild plant and animal populations e.g., St John's wort (Buckley, Briese & Rees
547 2003); Soay sheep (Ozgul et al. 2009); yellow-bellied marmots (Ozgul et al. 2010).
548 When sufficient data are available to develop mechanistic demographic models, the
549 assumption that the state variables chosen are good proxies of the environmental
550 effects on phenotypic traits should be tested. If, as in our study, the state variables
551 only encompass a small portion of the effect of the environment, then additional

552 environmental variables may need to be measured and included as predictors. Several
553 IPMs (e.g. Ozgul et al 2012, Coulson 2011) and physiologically structured population
554 models (e.g., Persson & de Roos 2006; Le Bourlot, Tully & Claessen 2014) accounted
555 for current environmental effects on life history and demography. Also these types of
556 models can implicitly account for delayed life-history effects because the past
557 environment can affect the current state of individuals and thus their life-history
558 trajectory (de Roos et al. 2003). However, an explicit consideration of the past
559 environment on demographic responses is so far missing, mainly due to the difficulty
560 of mechanistically modeling delayed life-history effects such as delayed density
561 dependence (Beckerman *et al.* 2003), and this is one of the main challenges left to be
562 achieved to improve the predictions of mechanistic demographic models.

563 Overall, body size and environmental variation are simply variables that were
564 convenient for answering the bigger question of how good is an easily observable,
565 individual state variable as a proxy for the nutritional effects of environments in a
566 population model. A comparative study using the approach presented here could offer
567 further refinement of our understanding of what kinds of organisms (e.g., capital vs.
568 income breeders) and patterns of environmental variations (e.g., magnitude and
569 temporal frequency of variation relative to generation time) are most likely to be
570 associated with a complex and limited ability of a single individual state variable to
571 predict demographic rates.

572 ## Data Accessibility

573 Data is available from Dryad Digital Repository:
574 http://dx.doi.org/10.5061/dryad.pq161

575

576 ## Acknowledgements

We thank L. Micallef, J. P. Dahlgren, U. Grömping, T. C. Cameron, and B. Bolker for helpful comments along the way. This research was supported by the European Research Council Starting Grant (#337785) and Nature Environment Research Council Grant (NE/I021594/1) to AO. Some appendices were created with knitr (Xie 2013).

Supporting Information

The following Supporting Information is available for this article online

Appendix S1: Details of Lab Experiments

Appendix S2: Density Calculations

Appendix S3: Model Selection and Full GAMM (R Code with Output)

Appendix S4: Decomposing Explanatory Power and Drawing Euler Diagrams (R Code with Output)

Appendix S5: Full GAM Fits and Splines (R Code with Output)

Figure S1: Effects of Past Environment

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